Limnologica 33, 92–98 (2003)

http://www.urbanfischer.de/journals/limno

LIMNOLOGICA

Food-web manipulation of drinking water reservoirs with salmonids: vertical distribution of prey and predator

Robert J. Radke*, Uwe Kahl, Jürgen Benndorf

Dresden University of Technology, Institute for Hydrobiology, Dresden, Germany

Received March 31, 2003 · Accepted May 8, 2003

Abstract

In a novel biomanipulation experiment salmonids were used as a tool to improve water quality. The manipulation was initiated in spring 2000 as a response to non-point sources of phosphorus in a drinking water reservoir in Saxony, Germany. Salmonids (brown trout, *Salmo trutta* forma *lacustris*) were chosen as predators as the reservoir has a large hypolimnic water body and surface temperatures rarely exceed 20 °C. The vertical distributions of prey fish and brown trout were analysed with a fleet of vertical gill nets set in the pelagic zone of the reservoir. Consumption of brown trout was estimated by means of a bioenergetic model and the diet analyses of the trout. While the dominant planktivore (roach, *Rutilus rutilus*) was caught almost exclusively in the epilimnion during the stratification period trout were caught mainly below a depth of 10 m. Diet analysis revealed that the trout performed vertical migrations to consume food in the epilimnic layer, as an important food component were adult terrestrial and aquatic insects. The amount of fish in the food increased strongly with the size of the brown trout. The consumption estimate suggested that the trout had consumed 2–3% of the total roach stock during the study period (May–November 2000) of the first year of biomanipulation. We conclude that in general salmonids are suitable for food-web manipulation in deep reservoirs, but the stocked fish should be as large as possible (> 300 mm) and the proportion of large trout (> 500 mm) should be as high as possible.

Key words: Brown trout – roach – perch – food-web – biomanipulation – vertical distribution – predation pressure – bioenergetics – consumption estimate

Introduction

Supplying high quality drinking water at reasonable costs remains the ultimate aim of all water suppliers (and customers). While this aim can easily be achieved in areas with sufficient precipitation and watersheds largely covered by woodland, areas with potential pollution sources (sewage, industry and agriculture) are frequently confronted with high costs concerning the water purification process. Within relatively short time scales watershed management can be very successful in reducing the input of nutrients from point sources into the tributaries of water reservoirs, but non-point sources often limit the success of such a management approach (CARPENTER et al. 1998). Being confronted with a relatively stable external nutrient load, internal mechanisms such as enhanced sedimentation and filtration and reduced internal loading become of greater importance (BENNDORF 1987; BENNDORF 1995). These internal mechanisms can be strongly increased by food-web manipulation (BENNDORF et al. 2002). A necessary prerequisite for a successful food-web manipulation with piscivorous fish is the

*Corresponding author: Robert J. Radke, Dresden University of Technology, Institute for Hydrobiology, Mommsenstr. 13, D-01062 Dresden, Germany; Phone: +49(351)463-32684, Fax: +49(351)463-37108, e-mail: radke@rcs.urz.tu-dresden.de

establishment of a multispecies piscivore community (BENNDORF et al. 1984), which is not constrained by ontogenetic bottlenecks (e.g. PERSSON 1988; OLSON et al. 1995) or morphological and behavioural characteristics of a single species (BENNDORF et al. 1984). Drinking water reservoirs are commonly situated in mountainous regions at higher elevations and this type of reservoir is characterised by lower average surface water temperature, a larger hypolimnic water body and a simply structured littoral zone compared to lowland reservoirs and lakes. These system-specific characteristics restrict the number of suitable piscivore species to those that show reasonable growth rates even at lower temperatures (e.g. salmonids). Experiments with salmonids as piscivores have usually been restricted to cases where either the yield of the stocked salmonids should be maximised (VEHANEN & ASPI 1996; VEHANEN 1997) or the individual growth rates of a population of stunted salmonids [i.e. arctic char, *Salvelinus alpinus* (LANGELAND 1990; DAMSGARD & LANGELAND 1994)].

Thus, in a novel whole lake experiment large salmonids (adult brown trout, *Salmo trutta* f. *lacustris*) were stocked as a food-web manipulation tool in a drinking water reservoir, with the aim to reduce unwanted zooplanktivorous fish (i.e. cyprinids). The goals of the study presented here were (i) to investigate the temporal course of the vertical distribution of prey and predator and (ii) to estimate the consumption of fish by the trout with the help of a bioenergetics model. Information on these two points is necessary to evaluate the efficacy of brown trout as a tool for biomanipulation in drinking water reservoirs.

Materials and Methods

Study site and fish community structure

The mesotrophic Saidenbach Reservoir is situated in the Erzgebirge (Saxony, Germany) at 439 m ASL (50°44′ N, 13°14′ E). The reservoir has a surface area of 1.46 km^2, a mean depth of 15.3 m and a maximum depth of 45 m. It is primarily used for drinking water supply and only to a limited extent for recreational fishing. Mean annual total phosphorus concentration declined from 25 µg L^{-1} to 15 µg L^{-1} within two years after the introduction of phosphate free detergents in the water shed in 1990 and has remained stable since (HORN et al. 1994; HORN et al. 2001). Despite the reduction in TP the average phytoplankton biomass has not declined to the same extent as the main limiting nutrient in the reservoir (HORN et al. 2001).

The fish community structure and food-web characteristics were assessed in 1999, 2000 and 2001 with standard bottom set gill net fleets (11 mesh sizes from 7 mm to 70 mm) set each month from April until November. The community was dominated by cyprinids (roach, *Rutilus rutilus* and bream, *Abramis brama*), while percids (perch, *Perca fluviatilis* and pike-perch, *Sander lucioperca*) formed less than 20% of the total fish biomass (Table 1). The total piscivore biomass (perch > 150 mm, pike-perch and pike, *Esox lucius*) was less than 20% of the total fish biomass. Brown trout were not caught during the assessment. A hydroacoustic survey performed in October 1999 estimated the fish stock at approximately 200 kg ha^{-1} (Simrad EY-200, HADAS post processing software). Roach was the main zooplanktivore in the reservoir and all size-classes fed primarily on the large bodied *Daphnia galeata* during summer and autumn (U. KAHL, pers. comm.). The reservoir was stocked with brown trout from March 2000 onwards (Table 2).

Vertical distribution and catch processing

The vertical distribution of potential prey (roach and perch) and predator (brown trout) was studied with a fleet of vertical gillnets, which were slightly modified from the original design used by HANSSON (1988) in the Baltic Sea. The width of each of the seven monofilament

Table 1. Biomass proportion (%) of fish species in Saidenbach Reservoir in 1999 and 2000 calculated from total catch per unit effort (CPUE) data.

Species	1999	2000
Roach	63.3	55.2
Bream	15.0	15.1
Perch	16.9	14.4
Pike-perch	0.0	1.1
Pike	2.3	0.7
Others	2.5	2.5
Brown trout	–	11.0

Table 2. Total biomass, mean total length and mean individual biomass of brown trout (*S. trutta* forma *lacustris*) stocked from 2000 to 2002 in the Saidenbach Reservoir.

Date	Total biomass (kg)	Mean total length (mm)	Mean biomass (g)
13.03.2000	350	358	663
08.04.2000	1560	346	599
07.04.2001	720	357	596
29.09.2001	200	301	360
22.11.2001	600	310	481
12.03.2002	1150	299	347
28.09.2002	230	317	276
03.10.2002	420	No data	No data

nets was 3 m and the depth 30 m. Mesh sizes ranged from 12 mm to 38 mm and were distributed in a geometrical order. The nets were exposed overnight in the centre of the reservoir at a depth of 30–33 m for 12 h twice a month from July to November in 2000 and from April to November in 2001. Fish were removed from the nets during the lifting process, separated into six depth steps (0–5 m, 5–10 m etc.) and cooled with ice until further processing. In order to detect seasonal influences on the vertical distributions the catch data were treated separately for the seasons without stable stratification (spring and autumn data pooled) and for the period of stable stratification (summer, epilimnic temperature ≥ 17 °C). Total length was measured to the nearest millimetre and wet weight (ww) to the nearest gramme. The stomachs of the trout were removed and frozen for further analysis. Scales from the region next to the pectoral fins of the trout were used for aging and back-calculation of growth. As the number of fish caught in the vertical gill nets was not sufficient to produce unbiased feeding data for the trout, additional fish from the standard gill nets were used for food analysis. Length frequency distributions of perch and roach were created from fish taken from the standard gill nets set in August 2000.

Food analysis and consumption estimate

The defrosted stomach contents were sorted into taxonomic groups and the volumetric proportion of each component was estimated visually with the help of a dissecting microscope. Fish remains were determined to species level, while all other components were grouped into the following categories: benthic invertebrates, adult terrestrial and aquatic insects (adults of several taxa termed as terrestrial insects), zooplankton and others (Oligochaeta, amphibian larvae and plant material).

A consumption estimate for the brown trout was performed for the period 01. May–30. November 2000 using the bioenergetics approach based on the balanced energy equation (Kitchell et al. 1977) implemented in the bioenergetics software (Hanson 1997). We used the same set of parameter values as Vehanen et al. (1998) had used for brown trout in their study except for the coefficient for temperature of maximum consumption where we used Elliot's original value of 18 °C (Elliott 1976b). As fish had not been tagged individually mass increase for this period was determined by back-calculating the length of 18 individuals at the start of the growing season (stocking), estimating their ww with the help of a length-mass regression established from the stocked fish and subtracting the calculated mass from their individual mass at the time of capture. The energy density of the brown trout was calculated according to an equation developed by Elliott (1976a) and ranged from 5026 Jg^{-1} (median value) at the time of stocking to

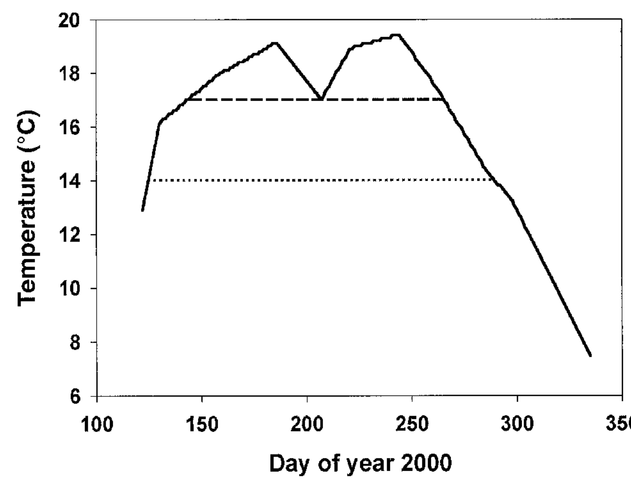

Fig. 1. Water temperature regimes used in the bioenergetic model for three different consumption estimates. Solid line represents epilimnic temperature in Saidenbach Reservoir in 2000, dashed line represents the 17 °C scenario and the dotted line the 14 °C scenario.

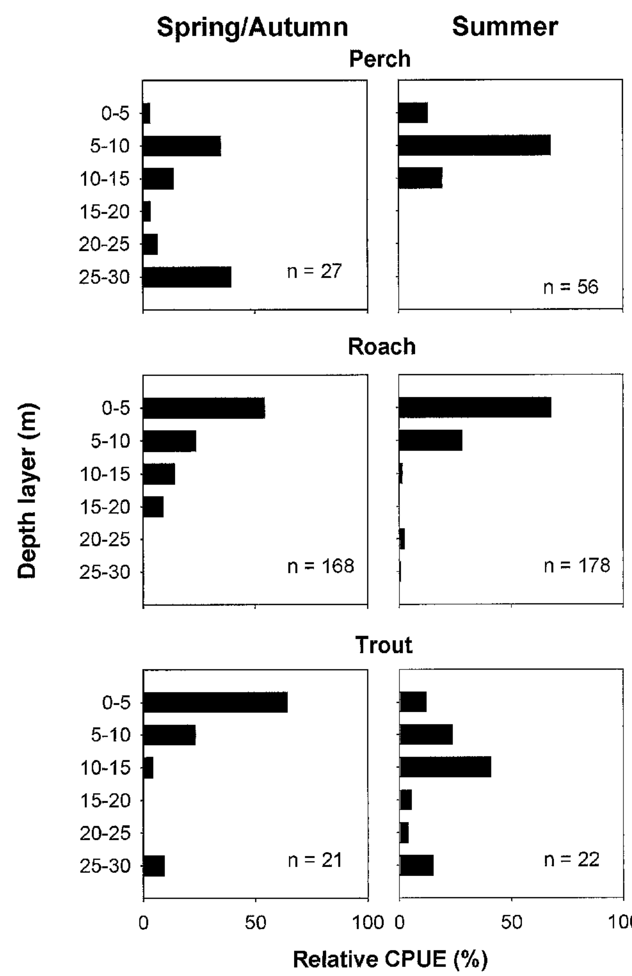

Fig. 2. Vertical distribution of perch, roach and brown trout in Saidenbach Reservoir in spring and autumn (pooled) and during summer stratification. Number of fish caught per season is shown in the graphs and proportion per depth layer of the total catch per season is given in relative catch per unit effort (CPUE).

4795 Jg^{-1} at the time of capture. Energy density of prey fish was set to an average value of 4000 Jg^{-1} and that of invertebrates to 3000 Jg^{-1} (see appendix in HANSON, 1997). To convert biovolume to biomass a specific weight of 1 g cm^{-3} was assumed to be realistic for all food organisms. We estimated total consumption for the period May–November 2000 at three different temperature scenarios. The first scenario assumed that during summer stratification the trout always remained at their preferred temperature of 14 °C (SCHULZ & BERG 1992). The second scenario assumed that trout performed diurnal vertical migrations during summer stratification (see "Results") and were exposed to varying temperatures resulting in an "average" temperature of 17 °C. The last scenario assumed that trout remained in the epilimnic layer throughout the period studied. All three temperature regimes are shown in Fig. 1.

Results

Vertical distribution

The vertical distribution of the three species reveals distinct seasonal patterns for each species (Fig. 2). During spring and autumn perch were distributed throughout the total water column. The two peaks can be attributed to separate size groups. While smaller (mostly juvenile) perch remained in the upper 15 m of the water column larger perch were found down to 30 m. In summer no perch were caught below 15 m and a clear maximum (69%) was found in the layer between 5 and 10 m. The largest proportion of roach was always caught in the surface layer, irrespective of season. During summer though the proportion caught above 10 m was 96% and that caught above 5 m was 70% of the total catch. The brown trout showed an inverse distribution pattern. While 86% of the trout were caught above 10 m depth in the spring/autumn periods, only 32% were caught above this depth during summer.

Food analysis, predator and prey size and consumption estimate

Fish prey was consumed by trout from April to August and in November (Fig. 3), though apart from August 2001 (only three stomach samples available) never exceeded 20% of the total food consumed. Identifiable fish remains were determined to be either perch or roach. Both species were represented in approximately equal proportions. Adult insects (mainly dipterans and mayflies) were the dominant food resource consumed in five of the seven months studied. Benthic invertebrates were consumed at higher proportions from April to July and zooplankton (mainly *Leptodora kindtii*) in June and

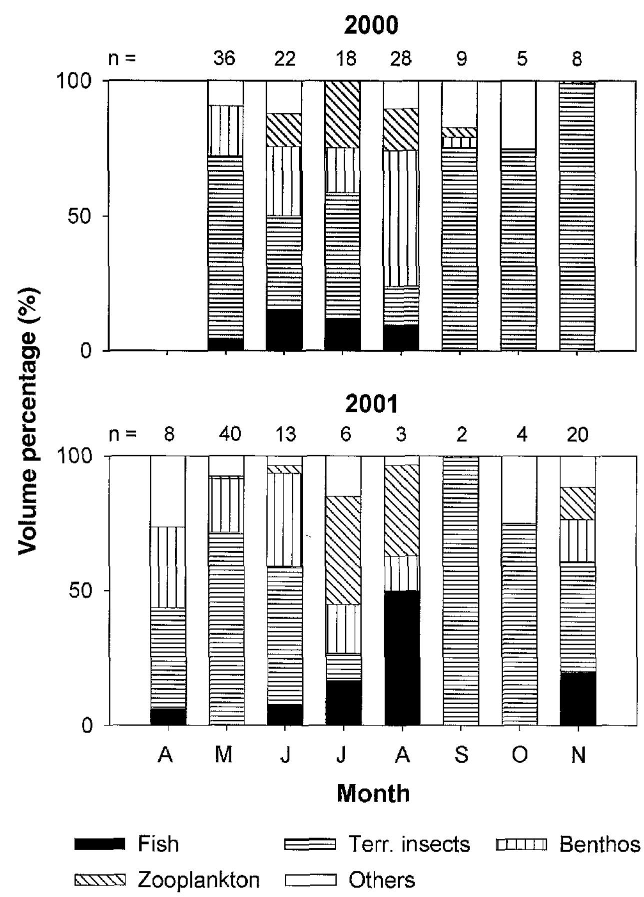

Fig. 3. Relative volume proportion of food components consumed by brown trout in Saidenbach Reservoir in 2000 and 2001 (n = number of stomachs analysed).

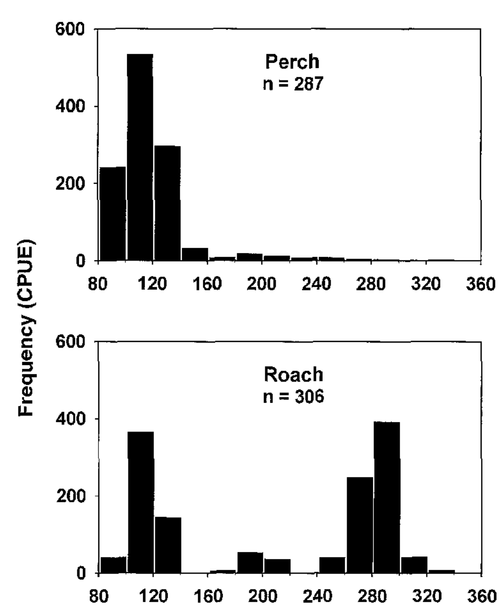

Fig. 4. Length-frequency distribution of perch and roach caught in Saidenbach Reservoir in August 2000.

August. The length frequency distribution of the two potential prey species perch and roach showed species specific differences (Fig. 4). While the most frequent size class of perch was that of fish in the length range of 100 to 120 mm, roach exhibited a bimodal distribution with one maximum in the same length range as perch and a further one in the length range of 280 to 300 mm. The trout showed a highly significant increase of piscivory with size (Spearman rank rs = 0.99, $p < 0.001$), with fish > 500 mm being more than 50% piscivorous (Fig. 5).

Mean monthly consumption of the trout varied up to more than twofold between the three scenarios (Fig. 6). Despite an overall decrease in the amount of food consumed the estimates of the 14 °C and 17 °C scenarios remained at a relatively stable ratio of 2:3 from May onwards. The scenario assuming that the trout remained in the upper parts of the water column throughout the year was strongly influenced by the critical thermal limits of the trout and consequently showed a strong decrease in the consumed biomass in those months with high epilimnic temperature (August and September). The total biomass of fish consumed per one kg of trout from May until November ranged from 244 g at the 14 °C scenario through 342 g at the 17 °C scenario to 441 g at the epilimnic scenario.

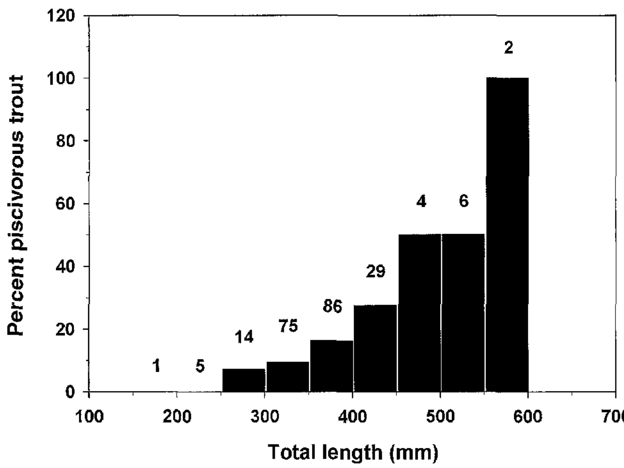

Fig. 5. Percent piscivorous brown trout per 50 mm length class caught in Saidenbach Reservoir in 2000 and 2001. Numbers above columns are number of trout with filled stomach analysed per length class.

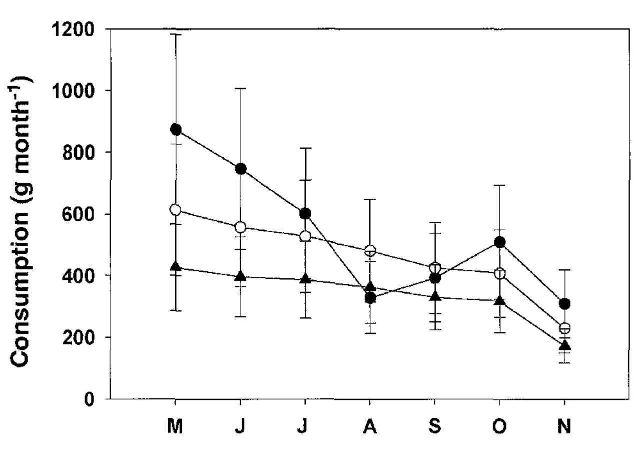

Fig. 6. Mean cumulative monthly consumption of 18 brown trout in Saidenbach Reservoir in 2000. The three lines are based on different temperature scenarios explained in the text (filled circles: epilimnic scenario; open circles: 17 °C scenario; filled triangles: 14 °C scenario; see also Fig. 1). Error bars denote 95% confidence level.

Discussion

Seasonal patterns in the vertical distribution of fish in temperate lakes are species specific and can primarily be attributed to physiological traits, whereas the actually observed patterns represent the trade-off between maximising energy gain and minimising predation risk (e.g. MAGNUSON et al. 1979; KEAST & FOX 1992; PERSSON et al. 1996). The patterns found in this study are in agreement with the published thermal requirements of the three species [e.g. THORPE (1977) for perch, HORPPILA & PELTONEN (1997) for roach and ELLIOTT & HURLEY (1999) for trout]. While the vertical seasonal migration of perch in deep lakes is well documented (ALLEN 1935; IMBROCK et al. 1996), to our knowledge no equivalent studies for roach populations living in lakes have been published. A study performed during summer stratification (BROSSE et al. 1999) found roach to be distributed in the uppermost water layer of a mesotrophic reservoir in France and is supported by our results. Field experiments with adult brown trout, which were tagged with transmitters, clearly showed that the fish preferred cooler water in thermally stratified lakes during the summer period (SCHULZ & BERG 1992; GARRETT & BENNETT 1995), though diel vertical migrations were not reported in these experiments. OLSON et al. (1988) found brown trout to be closely distributed just above the thermocline in Lake Ontario. The main prey fish were alewives (*Alosa pseudoharengus*), which were caught at a much higher mean water temperature than the brown trout (17.4 °C versus 13.4 °C), indicating that brown trout probably performed vertical migrations to catch their prey.

The proportion of fish in the food of salmonids generally increases with size and salmonids in lakes start to feed on fish at smaller sizes than those living in streams (KEELEY & GRANT 2001). Our results corroborate these results concerning the increase of piscivory with increasing predator size. Thus, unlike other piscivores (e.g. pike-perch) there is no size-related niche shift from e.g. planktivory to piscivory within their first year of life, but a more gradual increase of the amount of fish consumed. Using the relationships presented in the study of KEELEY & GRANT (2001), one would have expected the trout in our study to be almost entirely piscivorous. Thus, the large proportion of invertebrate prey in the food of the trout very likely reflects the limited availability of suitably sized prey fish in the reservoir in 2000. Although brown trout may swallow prey fish up to 41% of their body length (VEHANEN et al. 1998) mean values are found in the range of 16% (VEHANEN et al. 1998) to 33% (L'ABÉE-LUND et al. 1992). In our case, the predicted mean prey fish size of an average sized trout (approx. 350 mm in 2000) would lie within the range of 56 mm to 116 mm, which is not entirely within the lower length range found for both perch and roach. Unfortunately, the number of well preserved fish remains found in our study was not sufficient for a quantitative analysis of prey fish length.

The three consumption estimates based on the different temperature scenarios demonstrate the strong effect of temperature on the relative magnitude of the realised consumption. While the epilimnic scenario is relatively unrealistic, it seems reasonable to believe that in fact the trout experienced a temperature regime somewhere within the two other temperature scenarios. Unfortunately, it was not feasible within this study to track the thermal histories of trout directly with implanted data loggers or indirectly by ultrasonic telemetry. The overall drop in estimated consumption is a consequence of the reduced condition factor of the trout at the end of the period studied in 2000 (R. J. RADKE, unpubl.). DAMSGARD & LANGELAND (1994) found a similar effect in their study and we agree with their assumption that the condition factor of the stocked trout was well above normal levels. With regard to the roach (approx. 110 kg ha^{-1}, estimated from the hydroacoustic survey) and trout biomass (18 kg ha^{-1}, according to stocked biomass in spring 2000) the cumulative consumption of roach by the trout would range from 2% (14 °C scenario) to 3% (17 °C scenario) of total roach biomass in the period studied during the first year of biomanipulation.

Based on the results of our study we suggest that the trout were food limited during the summer period and thus were forced to forage under the suboptimal thermal conditions found in the epilimnic layer. Despite the small amount of fish observed in the food of the trout we think that the brown trout in the Saidenbach Reservoir have the potential to be piscivorous to a much higher degree. Apart from the strong correlation between length and proportion of piscivorous trout found in our study, this belief rests further on our own observations in the autumn of 2001, where trout were preying on 0+ cyprinids in the littoral zone and on a study by NIVA (1999), where trout performed a relatively fast switch from invertebrate prey to fish prey, as soon as this became abundant. We finally conclude (i) that for an effective food-web manipulation stocked brown trout must be relatively large (> 300 mm), (ii) that a high proportion of large trout (> 500 mm) must be present and (iii) that their proportion of the total fish community should be close to the upper limit of the range of 30–40% recommended by BENNDORF (1995) for successful biomanipulation.

Acknowledgements

We thank Falk Wieland for technical assistance in the field and Hans-Peter Uhlig (Talsperrenmeisterei Freiberger Mulde/ Zschopau) for providing the temperature data. The cooperation of the Anglerverband Südsachsen Mulde/Elster e.V. is greatly acknowledged. Two anonymous referees gave helpful comments to improve the manuscript, we are grateful for these. This study was supported by the Landestalsperrenverwaltung Sachsen and the Arbeitsgemeinschaft Trinkwassertalsperren e.V. (ATT).

References

ALLEN, K. R. (1935): The food and migration of the perch (*Perca fluviatilis*) in Windermere. J. Anim. Ecol. **4**: 264–273.

BENNDORF, J. (1987): Food web manipulation without nutrient control: A usefull strategy in lake restoration? Schweiz. Z. Hydrol. **49**: 237–248.

BENNDORF, J. (1995): Possibilities and limits for controlling eutrophication by biomanipulation. Int. Revue ges. Hydrobiol. **80**: 519–534.

BENNDORF, J., BÖING, W., KOOP, J. & NEUBAUER, I. (2002): Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. Freshw. Biol. **47**: 2282–2295.

BENNDORF, J., KNESCHKE, H., KOSSATZ, K. & PENZ, E. (1984): Manipulation of the pelagic food web by stocking with predacious fishes. Int. Revue ges. Hydrobiol. **69**: 407–428.

BROSSE, S., DAUBA, F., OBERDORFF, T. & LEK, S. (1999): Influence of some topographical variables on the spatial distribution of lake fish during summer stratification. Arch. Hydrobiol. **145**: 359–371.

CARPENTER, S. R., CARACO, N. F., CORRELL, D. L., HOWARTH, R. W., Sharpley, A. N. & Smith, V. H. (1998): Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. **8**: 559–568.

DAMSGARD, B. & LANGELAND, A. (1994): Effects of stocking of piscivorous brown trout, *Salmo trutta* L., on stunted charr, *Salvelinus alpinus* (L.). Ecol. Freshw. Fish **3**: 59–66.

ELLIOTT, J. M. (1976a): Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. J. Anim. Ecol. **45**: 273–289.

ELLIOTT, J. M. (1976b): Energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. **45**: 923–948.

ELLIOTT, J. M. & HURLEY, M. A. (1999): A new energetics model for brown trout, *Salmo trutta*. Freshw. Biol. **42**: 235–246.

GARRETT, J. W. & BENNETT, D. H. (1995): Seasonal movements of adult brown trout relative to temperature in a coolwater reservoir. N. Am. J. Fish. Manage. **15**: 480–487.

HANSON, P. C. (1997): Fish bioenergetics. University of Wisconsin – Madison Center for Limnology and University of Wisconsin Sea Grant Institute.

HANSSON, S. (1988): A simple vertical gill net system for variable current conditions. Hydrobiologia **160**: 107–110.

HORN, H., PAUL, L. & HORN, W. (2001): Phytoplanktonzunahme trotz fallender P-Belastung – ein Widerspruch? Ursachen der unerwarteten Entwicklung in einer Trinkwassertalsperre. gwf-Wasser/Abwasser **142**: 268–278.

HORN, W., HORN, H. & PAUL, L. (1994): Long-term trends in the nutrient input and in-lake concentrations of a drinking water reservoir in a dense populated catchment area (Erzgebirge, Germany). Int. Revue ges. Hydrobiol. **79**: 213–227.

HORPPILA, J. & PELTONEN, H. (1997): A bioenergetic approach on food consumption of roach (*Rutilus rutilus* (L.)) in a eutrophic lake. Arch. Hydrobiol. **139**: 207–222.

IMBROCK, F., APPENZELLER, A. & ECKMANN, R. (1996): Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and in situ observations. J. Fish Biol. **49**: 1–13.

KEAST, A. & FOX, M. G. (1992): Space use and feeding patterns of an offshore fish assemblage in a shallow mesotrophic lake. Environ. Biol. Fishes **34**: 159–170.

KEELEY, E. R. & GRANT, J. W. A. (2001): Prey size of salmonid fishes in streams, lakes, and oceans. Can. J. Fish. Aquat. Sci. **58**: 1122–1132.

KITCHELL, J. F., STEWART, D. J. & WEININGER, D. (1977): Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1922–1935.

L'ABÉE-LUND, J. H., LANGELAND, A. & SAEGROV, H. (1992): Piscivory by brown trout *Salmo trutta* L. and arctic charr *Salvelinus alpinus* (L.) in Norwegian lakes. J. Fish Biol. **41**: 91–101.

LANGELAND, A. (1990): Biomanipulation development in Norway. Hydrobiologia **200**: 535–540.

MAGNUSON, J. J., CROWDER, L. B. & MEDVICK, P. A. (1979): Temperature as an ecological resource. Am. Zool. **19**: 331–343.

NIVA, T. (1999): Relations between diet, growth, visceral lipid content and yield of the stocked brown trout in three small lakes in northern Finland. Ann. Zool. Fennici **36**: 103–120.

OLSON, M. H., MITTELBACH, G. G. & OSENBERG, C. W. (1995): Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology **76**: 1758–1771.

OLSON, R. A., WINTER, J. D., NETTLES, D. C. & HAYNES, J. M. (1988): Resource partitioning in summer by salmonids in south-central Lake Ontario. Trans. Am. Fish. Soc. **117**: 552–559.

PERSSON, L. (1988): Asymmetries in competitive and predatory interactions in fish populations. In: B. EBENMANN & L. PERSSON (eds.), Size-structured populations. Berlin.

PERSSON, L., ANDERSSON, J., WAHLSTROM, E. & EKLÖV, P. (1996): Size-specific interactions in lake systems: Predator gape limitation and prey growth rate and mortality. Ecology **77**: 900–911.

SCHULZ, U. & BERG, R. (1992): Movements of ultrasonically tagged brown trout (*Salmo trutta* L.) in Lake Constance. J. Fish Biol. **40**: 909–917.

THORPE, J. E. (1977): Morphology, physiology, behavior, and ecology of *Perca fluviatilis* L. and *Perca flavescens* MITCHILL. J. Fish. Res. Board Can. **34**: 1504–1514.

VEHANEN, T. (1997): Fish and fisheries in large regulated peaking-power river reservoirs in northern Finland, with special reference to the efficiency of brown trout and rainbow trout stocking. Regul. Riv. **13**: 1–11.

VEHANEN, T. & ASPI, J. (1996): Classification of northern Finnish lakes and the suitability for the stocking for brown trout (*Salmo trutta* (L.) m. *lacustris*). Fish. Res. **27**: 37–49.

VEHANEN, T., HYVARINEN, P. & HUUSKO, A. (1998): Food consumption and prey orientation of piscivorous brown trout (*Salmo trutta*) and pikeperch (*Stizostedion lucioperca*) in a large regulated lake. J. Appl. Ichthyol. **14**: 15–22.